REPRODUCTION OF THE BAY SCALLOP, AEQUIPECTEN IRRADIANS LAMARCK. INFLUENCE OF TEMPERATURE ON MATURATION AND SPAWNING[1]

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Influence of temperature on reproduction of marine invertebrates has been extensively reported in the literature. In many of these studies, reproductive cycles and spawning periods were described for a population of a species in one geographical area. Orton (1920) considered temperature as the most important factor for regulation of breeding in marine animals. Although he indicated that under normal conditions breeding temperature for a species is a physiological constant throughout the range, subsequent workers have demonstrated that latitudinally separated populations of a species breed at different temperatures (Loosanoff, 1956; Korringa, 1957). Hutchins (1947) stated that critical sea temperature for both reproduction and completion of the life cycle plays an important role in defining the distributional range of a species.

The differences in reproduction and larval ecology of widely distributed marine invertebrates are discussed in detail by Thorson (1950). The variation in reproductive physiology at different latitudes of some marine invertebrate species has been discussed in a recent review by Giese (1959). Loosanoff (1956) studied the temperature requirements for maturation and spawning for transplanted southern populations of *Crassosstrea virginica* in northern waters. Experimentally, the gonads of *C. virginica* and *V. mercenaria* were ripened in winter and the larvae were reared in the laboratory (Loosanoff and Davis, 1950, 1952). Turner and Hanks (1960) reported stimulation of gametogenesis in *Hydroides dianthus* and the bay scallop, *Pecten irradians,* during winter at higher temperature in the laboratory.

Aequipecten irradians Lamarck has a wide geographic distribution along the Atlantic and Gulf coasts of the United States, resulting in widely separated populations being exposed to different temperature regimes. In addition, morphological differences between populations have been reported and it is possible that physiological differences also exist (Abbott, 1954; Sastry, 1961). The present investigation was undertaken to study the influence of temperature on maturation of gametes and spawning of a population of bay scallops from Florida. These results were compared with data obtained on more northern populations by Belding (1910), Gutsell (1930) and Marshall (1960)

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Materials and Methods

The animals were obtained from grass flats in Alligator Harbor, Franklin County, Florida. Determination of the natural reproductive cycle was made on samples of animals collected at monthly intervals. The gonadal condition was determined by microscopic examination and gross observations of the coloration of the gonad. On the basis of these two criteria, the functionally bisexual gonad was classified into one of six stages of development. These stages are described in detail below. Animals obtained from their natural environment were also maintained in the laboratory in running sea water at 23.0 ± 1.0° C. for the purpose of studying the influence of temperature on gonadal maturity and spawning.

Spawning was induced in mature animals in the laboratory, by heating. Mature scallops were placed in fingerbowls containing sea water of the same temperature as that at which they had been maintained. The temperature of the sea water was gradually raised to 30° C., by heating with a 115-watt lamp, and allowed to cool gradually. The temperature of the sea water in the bowl at the time the animal spawned was recorded and is considered as the spawning temperature. The procedure for stimulation of spawning in the laboratory was as shown in Table I, to study the effect of changing temperature and light on gamete liberation.

Table I

Method of changing temperature and light to stimulate spawning in the bay scallops in the laboratory

Bowl	Temperature °C.	Light
1	Initial increase and later cooling	exposed
2	Increase only	exposed
3	No increase or decrease	exposed
4	Initial increase and later cooling	not exposed
5	Increase only	not exposed
6	No increase or decrease	not exposed

Observations and Results

Morphological differences in geographic populations

Aequipecten irradians Lamarck is a polytypic species according to the classification of Dodge (1952) and Abbott (1954). Three subspecies, *A. irradians irradians* Lamarck, *A. irradians concentricus* Say and *A. irradians amplicostatus* Dall are recognized, based on the ecology and morphological characters of different geographic populations.

Rib counts on the outer side of the left valve were made for the Alligator Harbor population and compared with those of specimens obtained from Beaufort, North Carolina, and Woods Hole, Massachusetts. While the number of ribs in the Alligator Harbor population varied between 18–24, 21 being the most common, Beaufort and Woods Hole scallops had 18–19 and 17–18, respectively.

The temperature zonation on the Atlantic coast of the United States has been shown by Fischer (1960), indicating the differences in summer and winter temperature ranges above and below Cape Hatteras. Scallops in the Woods Hole region are subjected to cold temperatures in winter whereas the Beaufort and Alligator Harbor scallops experience much warmer temperatures throughout the year.

Reproductive cycle

The gonad condition of bay scallops obtained from Alligator Harbor is classified into stages I–VI. Stages I–III are immature, IV is mature, and V–VI are partially spent and spent conditions. Stage I gonad is small and transparent, and the only reproductive tissues that were observed were narrow tubules with primary germ cells. The stage II gonad has increased in size and is translucent. In gross examination, testicular and ovarian regions could not be distinguished; however, microscopic examination revealed that a few follicles had developed spermatogonia and oogonia. The gonad in stage III began to fill in with spermatogonia and oogonia

TABLE II

Gonad condition of bay scallops during 1957–1958

Month	Number examined	Condition of gonads per cent		
		Immature stages I, II, III	Mature IV	Spent V, VI
November, 1957	5	100	0	0
December	—	—	—	—
January, 1958	36	100	0	0
February	133	100	0	0
May	4	100	0	0
June	148	94.6	5.4	0
July	166	53.6	46.4	0
August	136	0	61.0	39.0
September	35	0	53.6	45.7
October	21	0	100.0	0
November	16	0	93.7	6.3
December	7	0	86.4	13.6

and it became enlarged in volume. The bisexual nature of the gonad could be seen from the proximal white testicular area and the distal pale orange ovarian portion. Spermatogonia increased in number and were in clumps. A few spermatozoa were also present. Many half-grown oocytes with stalks and a large germinal vesicle were observed.

The stage IV gonad has increased considerably in volume, with round margins; it contained thickly packed follicles. The testicular and ovarian portions were cream and bright orange, respectively. Microscopic examination showed free, active spermatozoa and mature pear-shaped oocytes. In the partially spent gonad condition (stage V), testis and ovary were differentiated by the pale white and orange colors of their respective regions. The gonads retained some residual mature genital products. Empty spaces in the follicles of stage V gonads distinguish them from stage III gonads. Completely spent stage VI gonads were light brown in

TABLE III

Stimulation of the bay scallops to maturity in running sea water in the laboratory

Date of collection	Number of animals used	Condition of the gonad at the time of collection	Temp. ° C.	Date spawned	Days to reach maturity (stage V)
7/27/58	15	stage III	30.0 ± 1.0	8/4/58	6
12/13/58*	20	stages II and III	23.0 ± 1.0	1/9/59	26
8/28/58	8	stage VI	29.0 ± 1.0	9/29/58	35

* This sample was maintained at higher temperature when the natural habitat temperatures were approximately 14° C. The other two observations were done at approximately identical temperatures as those in the natural habitat during that period of the year.

color, with no differentiation between testicular and ovarian regions. The gonads were shrunken and flaccid with empty follicles. The changes in gonadal condition of bay scallops obtained from Alligator Harbor during 1957–1958 are shown in Table II.

Influence of temperature on gonad maturity

Scallops, 30–35 mm. long, obtained from their natural habitat during December when the water temperature was 14° C., were maintained in running sea water at two experimental temperatures. A control group was maintained at 14° C. and another batch was maintained at 23 ± 1.0° C. The only food available to the animals during this period was that which was circulating in the laboratory sea water system. Scallops maintained at the higher temperature reached stage IV in 26 days while the gonadal condition of those kept at 14° C. remained the same (Table III). The scallops which matured at the elevated temperature spawned successfully and the resultant larvae were cultured in the laboratory.

Observations on the reproductive cycle of animals from the field showed that most of the animals reached stage II or III by the beginning of winter. They remained in this condition throughout the cooler months (Table I) and resumed

TABLE IV

Average monthly temperature and salinity during 1957–1958 in Alligator Harbor, Florida

Month	Temperature ° C.	Salinity ‰
June, 1957	30.0	27.5
July	29.0	31.8
August	31.8	
February, 1958	8.9	
April	19.4	29.5
June	30.1	26.6
July	31.5	28.1
August	29.2	29.3
September	28.9	30.0
October	24.2	31.3
November	22.0	
December	13.6	32.4

development with the rising spring temperatures. Apparently low temperatures slowed maturation of gonads because population samples collected and maintained in the laboratory at elevated temperatures spawned successfully. Temperature and salinity data from Alligator Harbor region during 1957–1958 are shown in Table IV.

Spawning period

Observations on gonad condition of bay scallops obtained from their natural habitat (Table I) indicate that the spawning period commences in Alligator Harbor region at the beginning of August. Peak spawning takes place during August and September. Some minor spawning continues beyond September but this seems to add little to the population. A correlation of peak spawning period with temperature data in the study area suggests that the bay scallops began spawning when temperature decreased after a summer maximum, at least in 1958.

Effect of temperature on spawning

Spawning of bay scallops in the laboratory was obtained only when the animals were subjected first to increasing temperatures and then decreasing temperatures. In all other experimental conditions mentioned in the methods section, no spawning

TABLE V

The effect of different maintenance temperatures on spawning temperatures of the bay scallops in the laboratory

Date spawned	No. animals spawned	Maintenance temperature ° C.	Increase in temperature ° C.	Spawning temperature ° C.	Nature of spawn
8/11/58	2	29.5	30.0	27.5	eggs
8/19/58	4	29.0	30.0	27.0	eggs
12/22/58	2	12.5	30.0	23.0	eggs
1/9/59	2	10.5	30.0	22.0	eggs
1/16/59	2	14.0	30.0	23.0	eggs
9/29/59	5	27.1	30.0	24.6	eggs, sperm
2/16/60	1	10.5	30.0	27.9	sperm
3/12/60	2	14.5	30.0	25.5	eggs

occurred. Addition of warm sea water and later cooling also induced spawning in most trials. It was not possible to induce spawning when the water temperature was increased to 30° C. without subsequent cooling. These laboratory observations on the effect of temperature on spawning are in agreement with the temperature conditions observed at the time of initiation of spawning period in nature. Apparently an initial gradual increase and a later decrease in temperatures are necessary to initiate spawning in bay scallops. Salinity does not vary widely in the study area. Laboratory observations also indicate that light conditions do not influence the spawning behavior in the bay scallops.

Spawning of bay scallops was partial in the laboratory. With only a few exceptions the spawn consisted of eggs only. When the animals liberated both sperm and eggs, there was a time lag between liberation of either eggs or sperm. Simultaneous liberation of both types of gametes was never observed in the laboratory-spawned scallops.

Laboratory spawning was induced during different months of a year. The animals used in these experiments were at different temperatures in the laboratory sea water prior to induction, with identical experimental procedures. The results of these observations are shown in Table V. The length of time and the temperatures at which the animals were in laboratory sea water tables before the experiments were not constant. The temperature at which the animals liberated gametes showed some interesting differences. The animals spawned during cooler months, in general liberated spawn at lower temperatures as compared with those from warmer months.

Discussion

The changes in the gonad cycle of the bay scallop collected during different months of 1957–1958 showed that maturity is reached towards the end of July and spawning commences at the beginning of August in Alligator Harbor, Florida. The beginning of spawning coincides with decreasing temperatures following a summer maximum during 1958.

The development of gonads to maturity is slowed during winter months in nature. Animals brought into the laboratory in December and maintained at elevated temperatures developed to maturity in 26 days from the time of introduction into the sea water tables. This suggests that perhaps a time-temperature relation exists in gonadal development of bay scallops to maturity, once the gametogenesis has been initiated in their natural habitat. Scallops reared from eggs in the laboratory at 24.5 ± 0.5° C. failed to initiate gametogenesis at the age of 3–4 months while a comparable age group from natural habitat showed primary germ cells.

There are too few experimental temperature observations at which the scallops matured in the laboratory to warrant any concrete conclusions regarding the factors that control reproduction. However, these limited observations suggest that maturation of bay scallops may be controlled by exogenous factors after initiation of gametogenesis in their natural environment.

Laboratory spawning of scallops shows that an initial increasing and subsequent decreasing of temperatures stimulate liberation of gametes. Results obtained from spawning of scallops during different months of a year showed some interesting differences in the temperature at which they spawned. These experiments have to be done with more critically controlled conditions to find out if there is an effect of temperature acclimation on spawning. These observations on spawning in the laboratory indicate that spawning of bay scallops is not restricted to a particular period in the year or to a critical temperature. It appears that spawning is dependent on the maturation condition of the gonads and a favorable external stimulus. These observations suggest the possibility that spawning of bay scallops is not entirely operated by endogenous factors but by a combination of internal and external factors.

A comparison of the available information on reproduction of bay scallops from more northern geographical areas (Belding, 1910; Gutsell, 1930) with the results obtained for a Florida population show some differences in peak reproductive period, spawning behavior and the temperature requirements for maturation. Belding (1910) reported that the gonads of bay scallops in Massachusetts reach maturity and commence spawning towards the middle of June when the water temperatures are approximately 14–16° C. Gutsell (1930), working with Beaufort, North Carolina, populations, stated that spawning commenced in August. Observation on scallops at Beaufort during the fall of 1961 showed that they reach maturity early in fall and commence spawning. As already stated the Florida population of scallops commences spawning at the beginning of August. The spawning period in these three geographic populations is different, and also the spawning stimulus appears to be different, especially in Massachusetts and Florida. Belding (1910) reported that the bay scallops in Massachusetts commence spawning with increasing temperatures. Gutsell (1930) noted that the Beaufort population commences spawning with decreasing temperatures in fall. Laboratory and field observations in the present study indicate that the Florida population commences spawning with decreasing temperature after an initial maximum.

A comparison of these observations on latitudinal populations permits some generalizations on the subspecies from Atlantic and Gulf Coasts. The temperature requirements for maturation and spawning of bay scallops from south of Cape Hatteras appear to be higher than those from further north. Differences in spawning behavior and peak spawning period also occur between the northern and southern populations. Loosanoff (1952, 1956) and Korringa (1957) showed that populations of some species of bivalve mollusks from different geographical areas show variations in their temperature requirements for maturation and spawning. Transplanted latitudinal populations of bay scallops would enable testing these physiological differences for reproduction and their adaptive value.

Summary

1. Subspecies *A. i. concentricus* from Alligator Harbor, Florida, reaches maturity towards the end of July when the summer temperatures are maximum and commences spawning early in August as the temperatures begin to decrease.

2. Winter temperatures slow gonadal development of a Florida population of scallops. During winter, scallops were stimulated to maturity at elevated temperature of $23.0 \pm 1.0°$ C. in 26 days.

3. Matured scallops maintained in the laboratory spawned in response to elevated temperature during different months of the year.

4. The subspecies *A. i. irradians* from Massachusetts and *A. i. concentricus* from Florida and North Carolina show differences in temperature requirements for maturation and spawning. The subspecies north of Cape Hatteras reproduce at lower temperatures as compared with the southern subspecies. The spawning of both the subspecies does not overlap.

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